The Ecology of Poole Harbour
John Humphreys and Vincent May (editors)

6. History and Ecology of *Spartina anglica* in Poole Harbour*

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Spartina anglica is a grass of saltmarshes and mudflats. It resulted from chromosome doubling in a hybrid between a native grass, *S. maritima*, and a species accidentally introduced from North America, *S. alterniflora*. The hybrid, *S. x townsendii*, was first recorded in 1870 near Hythe in Southampton Water; *S. anglica* was first recorded in 1892 from Lymington. *Spartina anglica* arrived in Poole Harbour in the 1890s, and by the early 1920s it covered over 800 ha of mudflats that had previously been largely clear of vegetation. During the late 1920s, *S. anglica* began to recede, and by 1980 about 350 ha remained. The rapid spread and decline of *S. anglica* was associated with physical and biological change within the harbour, the most noticeable being changes in the depth of navigation channels and the colonization of pure swards of *S. anglica* by other saltmarsh plants. The spread of *S. anglica* is also implicated in local reductions in the populations of wading birds.

Introduction

Poole Harbour is one of the most important features in the natural history of Dorset. It was formed when a post-glacial rise in sea level submerged land surrounding a 'Solent River', which flowed eastwards across land that is now Poole Bay (Bird and Ranwell, 1964). The Rivers Frome and Piddle, which flow into Poole Harbour at Swineham, are the headstreams of that river. The area of Poole Harbour was greatest about 6000 years ago, since when natural sedimentation and land reclamation have reduced the area by about 1000 ha to the present 3600 ha (May, 1969; Gray, 1986a).

Although urban development has affected the edges of the harbour, a probably more significant change occurred within the body of the harbour in the last 100 years by natural means. In the 1890s, mudflats began to be colonized by a perennial grass called *Spartina anglica* (hereafter *Spartina* unless stated otherwise). *Spartina* spread very quickly in the harbour and covered over 800 ha by 1924. For various reasons, there has since been much loss of *Spartina*, and the species now covers less than 400 ha (Gray *et al*., 1991). This chapter examines some of the effects that the changes in the distribution of *Spartina* have had on the hydrography and ecology of Poole Harbour.

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The origin of *Spartina anglica*

Spartina anglica is a textbook example of the evolution of a new species by allopolyploidy, the hybridization of two species to give a fertile new species with about twice the mean chromosome number of the parental species. An allopolyploid can be formed either by the fusion of diploid gametes or by chromosome doubling in a (usually sterile) F_1 hybrid.

The '*Spartina* story' (Lambert, 1964) began with the accidental introduction of *Spartina alterniflora*, a plant of the eastern seaboard of North America, into Southampton Water sometime before 1816. At Hythe, and at the mouth of the Itchen, *S. alterniflora* grew close to *S. maritima*, a native plant that is now extinct in Southampton Water (Townsend, 1883; Raybould *et al*., 1991b). In about 1870, a new form of *Spartina* was collected at Hythe. This *Spartina* spread slowly in Southampton Water until the late 1880s when "something occurred that favoured the spreading of the grass" (Stapf, 1913). All the morphological, cytological and biochemical evidence (Marchant, 1967, 1968; Raybould *et al*., 1991a) suggests that the new *Spartina* was a sterile hybrid between *S. alterniflora* and *S. maritima* (with *S. alterniflora* as the female parent (Ferris *et al*., 1997)) and the 'something that favoured the spreading' was chromosome doubling in the hybrid, which produced a fertile allopolyploid able to spread by seed.

The F_1 hybrid is named *Spartina* x *townsendii*, and is still abundant at Hythe and also occurs in small patches scattered throughout the British Isles. The fertile allopolyploid is named *S. anglica*. This species spread along the south coast of England and the north coast of France by the natural dispersal of seeds and plant fragments (Oliver, 1920, 1925). *Spartina anglica* was planted extensively on mudflats in other parts of the British Isles, in north-west Europe and in several other countries (notably Australia and China) for coastal defence and land reclamation (Ranwell, 1967).

The spread of *Spartina anglica* in Poole Harbour

Hubbard (1965) gives 1890 as the date of the first appearance of *Spartina* in the harbour, although this is an estimate based on anecdotal evidence in the personal correspondence of local residents. Oliver (1925) gives 1899 as the first confirmed record. Seedlings and plant fragments of *Spartina* established on driftlines or flat mud by being trapped in mats of eelgrass (*Zostera* spp.) (Hubbard, 1965). Once established, plants spread vegetatively at "several feet" per year (Oliver, 1925), particularly in the bays and inlets of the southern shore west of Ower (Hubbard, 1965). The leeward sides of islands and mudflats in the Wareham Channel were also colonized rapidly. The most dramatic spread was in Holes Bay, where 63% of the intertidal zone became covered with *Spartina* between 1901 and 1924 (Gray and Pearson, 1984). On the north shore of the harbour to the east of Holes Bay, there was little growth of *Spartina*, apart from sheltered sites in Parkstone Bay (Hubbard, 1965). In general, towards the mouth of the harbour, *Spartina* remained as disconnected clumps and in the centre of the harbour, swards formed on the fringes of bays. Only in the upper reaches of the harbour, west of a line from Fitzworth Point to Hamworthy, was there extensive sward formation (Hubbard, 1965).

The seaward limit for successful establishment of *Spartina* in Poole Harbour was about Ordnance Datum (Newlyn) (Hubbard, 1965). This limit is much lower than other estuaries on the south and west coasts of Great Britain and is probably due to the small spring tidal range in the harbour (Gray *et al*., 1991). The upper limit varies between +0.5 m OD (e.g. in Brands Bay) and +0.9 m OD (e.g. Keysworth and Arne Bay) (Ranwell *et al*., 1964).

Spartina reached its maximum area in Poole Harbour between 1917 and 1924, at which time it covered about 800 ha (Gray *et al*., 1991). However, by 1919, some *Spartina* marsh was being eroded, possibly due to the migration of a creek (Oliver, 1920). The rate of loss increased during the 1920s as marshes in exposed locations were subject to tidal scour (Oliver, 1925). Marshes either side of Wych Channel at Shipstal Point were particularly affected in the early 1920s (Hubbard, 1965).

Between 1924 and 1952, there was some spread of *Spartina* on the south-west shore of the harbour and along the shores of the Wareham Channel. However, the general trend was recession of *Spartina*, particularly along the south-east shore and areas around Brownsea Island and in Holes Bay (Table 1). Hubbard (1965) estimated that there was a net loss of 172 ha of *Spartina* marshes between 1924 and 1952. Gray *et al*. (1991) used different methods and estimated 200 ha of *Spartina* were lost from the harbour between 1924 and 1952.

Gray and Pearson (1984) estimated that 250 ha of *Spartina* were lost between 1952 and 1980, leaving about 350 ha. The most severe recession occurred in areas east of the Arne peninsula, particularly around Furzey Island, to the west of Green Island and in Brands Bay. Smaller reductions took place around Long and Round Island and in the Middlebere Channel. *Spartina* was also lost from Holes Bay during this period (Table 2).

Recent figures are available for Holes Bay only (Table 2) and show *Spartina* is still receding. The main changes between 1981 and 1994 are the reduction in area of the intertidal area because of reclamation for the Holes Bay road, and continued fragmentation of the *Spartina* marsh on the spit extending south into the bay from the centre of the railway causeway.

There are several reasons for the loss of *Spartina* in Poole Harbour. The first is erosion at the edges of marshes. This began in the 1920s (see above) and is still continuing, being particularly prevalent between Holton Heath and Rockley Sands. Gray and Pearson (1984) found that loss of *Spartina* between 1952 and 1980 was due to the break-up of marsh on intertidal mudflats, rather than on the marshes fringing land.

Another important cause is ‘die-back’, where *Spartina* degenerates in patches in the body of a sward, rather than at an eroding edge. The cause of die-back is still not known completely, although the process seems to be associated with badly drained, highly

Table 1 Estimated loss/gain in area of *Spartina* in Poole Harbour

	Date of establishment (E) and/or sward completion (S)	1924	1952	Loss/gain
Brands Bay	S 1914	75.5	80.4	+4.9
Whitley Lake	E 1901	1.2	4.0	+2.8
Furzey and Green Island		76.4	45.0	-31.4
Southern Shore (east)	S 1914	101.0	73.4	-27.6
Southern Shore (west)	E 1890 S 1913–14	102.1	123.2	+21.1
Parkstone Bay	E 1901	37.1	2.2	-34.9
Adjacent to Brownsea Island		52.3	0	-52.3
Long and Round Island and Grip Heath	S 1914	67.8	53.8	-14.0
Arne Bay	E 1898 S 1915	30.2	40.6	+10.4
Holton - Rockley	E 1907	24.7	26.8	+2.1
Holton Mere (Keysworth)	E 1912	26.4	43.8	+17.4
Giggers' Island and Swineham	E 1915	0.4	11.9	+11.5
Holes Bay	E 1901 S 1924	227.7	140.4	-87.3
Lytchett Bay	E 1910	44.1	43.8	-0.3
Brownsea Island	E 1930	0	5.4	+5.4
Total		866.9	694.7	-172.2

Source: Hubbard (1965).

Table 2 Area of Poole Harbour covered by *Spartina*

Date	Area in whole harbour	Area in Holes Bay (proportion of intertidal)
1924	800	208 (0.63)
1952	600	132 (0.41)
1972		95 (0.32)
1980	350	80 (0.29)
1994		63 (0.25)

Source: Pre-1990 data from Gray *et al.* (1991) and Gray and Pearson (1984) who used slightly different methods from Hubbard (1965).

anaerobic soils in which the *Spartina* rhizomes may be poisoned by sulphide ions and lack of oxygen (Goodman and Williams, 1961; Gray *et al*., 1991). Die-back also began in Poole Harbour in the 1920s and is thought to be the principal cause of the large reduction of *Spartina* in Holes Bay (Hubbard, 1965). Die-back is still occurring in parts of the harbour, in Brands Bay, for example.

Finally, *Spartina* marsh has been lost through invasion by other species from the landward edge. Invasion is characteristic of marshes to the west of Arne (Gray and Pearson, 1984), where large areas have been replaced by *Phragmites communis* (common reed) in areas with low salinity (Ranwell *et al*., 1964; Gray, 1986a). Other species that have invaded the *Spartina* sward at Keysworth are *Scirpus maritimus* (Sea Club-rush), *Elytrigia atherica* (Sea Couch Grass), *Agrostis stolonifera* (Creeping Bent), *Festuca rubra* (Red Fescue) and *Puccinellia maritima* (common saltmarsh grass) (Hubbard and Stebbings, 1968). *Spartina* swards have also been invaded by *Atriplex portulacoides* (Sea Purslane) and *P. maritima* in, for example, Parkstone Bay, Lytchett Bay, Brands Bay and in Middlebere and Wych Channels (Gray, 1986a).

Poole Harbour is the source of much of the *Spartina* planted in the British Isles and abroad for coastal defence and land reclamation. In the 1920s, 40,000 plants of *Spartina* were exported from Poole to Holland for reclamation following a successful trial of 50 plants by the Dutch government. In 1929, the Ministry of Agriculture published a pamphlet on the uses of *Spartina* which generated world-wide interest and many requests for plant material. Up to 1936, over 35,000 plants were exported from Manningtree (Essex) populations that originated from plants taken from Poole Harbour in 1924. Between 1928 and 1936, over 85,000 plants were exported directly from Poole to sites in Ireland (16,000 plants to 12 sites), the UK (30,000 plants to 26 sites), Germany (20,000 plants), Denmark (7000 plants) and several other countries including Australia and Trinidad. Hubbard (1965) estimated that between 1924 and 1936, over 175,000 plants and many seed samples were sent from Poole to at least 130 sites around the world. The outcome of these introductions is described by Ranwell (1967).

Most of the *Spartina* in Poole Harbour is the fertile allopolyploid, *S. anglica*. However, the sterile F_1 hybrid, *S.* x *townsendii* has also been found. In the 1960s, Hubbard (1965) recorded *S.* x *townsendii* from the landward side of marshes in Arne Bay, to the east of Fitzworth Point, at Ower, from both sides of Goathorn Point and Keysworth. Small patches were also found at Holes Bay, Brands Bay, Whitley Lake, Furzey Island and Green Island. Isolated tussocks also occurred on the seaward side of the Keysworth marsh. No systematic search has since been made for *S.* x *townsendii*, although clones have been found in Brands Bay with very high tiller density, which is characteristic of this species. The *S.* x *townsendii* plants in Holes Bay have almost certainly been lost following reclamation for development at Fleetsbridge and for the Holes Bay road. It is notable that *S.* x *townsendii* was particularly prevalent at Arne, because it is from this area that much *Spartina* was exported. The dispersal of *Spartina* from Poole may explain the occurrence of *S.* x *townsendii* in Norfolk and Ireland (Hubbard, 1965).

Hydrographical change associated with *Spartina*

Spartina has greatly affected the sedimentation regime of the harbour (for detailed accounts see Bird and Ranwell, 1964; Ranwell, 1964; Hubbard and Stebbings, 1968), first by accreting and consolidating sediment by rhizome growth, and then by releasing this sediment as the sward eroded and died-back. In its period of expansion, *Spartina* accreted sediment rapidly. Hubbard and Stebbings (1968) estimated that locally in the upper harbour up to 1.8 m of sediment was trapped by *Spartina*. In other parts of the harbour, depths of 70–100 cm were common, dropping to 35 cm near the harbour mouth.

Only a small proportion of the sediment accreted by *Spartina* entered the harbour during the accretion process. Hubbard and Stebbings (1968) estimated that about 1 million tons of sediment were trapped by *Spartina* in the upper harbour over 55 years. During this time, the amount of sediment brought into the harbour by the River Frome was about 40,000 tons (1/25th of the total). The main hydrographical effect of the expansion of *Spartina* was, therefore, the stabilization of previously mobile sediment, rather than the accretion of new material. This stabilization led to a deepening of many navigation channels between the 1849 and 1934 hydrographical surveys of the harbour (Figure 1 and Table 3).

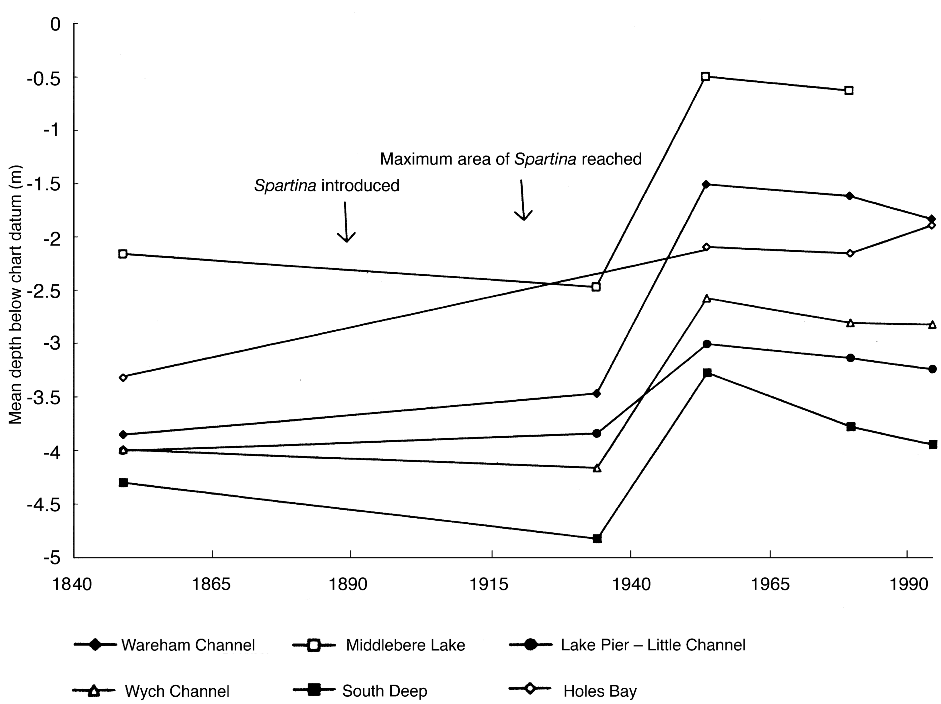

Figure 1 Changes in the mean depth of channels in Poole Harbour.

Table 3 Depths of navigation channels in Poole Harbour

	Mean channel depth (m)				
	1849	1934	1954	1980	1995
Main harbour					
Lake Pier - Little Channel	4.00	3.85	3.02	3.16	3.28
Middlebere Lake	2.16	2.48	0.51	0.65	*
South Deep	4.30	4.83	3.29	3.80	3.98
Wareham Channel	3.85	3.48	1.52	1.64	1.87
Wych Channel	3.99	4.17	2.59	2.83	2.86
	1849		1952	1980	1995
Holes Bay - Backwater Channel					
East Arm	2.49		1.09	1.67	0.72
West Arm	3.55		1.26	0.99	0.76
South Arm	3.50		3.43	3.46	3.88

*No survey as channel too shallow.

Source: Pre-1995 *Spartina* cover from Gray *et al.* (1991).

The die-back and erosion of *Spartina* caused an enormous amount of sediment to be released back into the harbour quickly (Green 1940). Between 1934 and 1954, there was considerable shoaling in all channels in the main harbour (Figure 1). In the long channels of the north and west part (Wareham and Wych), shoaling was greatest in the upper parts. For example, the average depth change in the lower 7000 feet of Wareham Channel was 3.17 m, while in the upper 4000 feet the average change was only 1.48 m (Figures 2 and 3). There was no survey of Holes Bay in 1934 but we can infer from the changes in other parts of the harbour that shoaling between 1849 and 1954 (Table 3) may have begun in the 1920s as the *Spartina* regressed.

Since 1954, the channels have deepened in most parts of the harbour (Figure 1 and Table 3), although the dredging of some of these channels was considered in the early 1980s (Poole Harbour Commissioners, 1982). South Deep may have deepened the most due to greater scouring near the harbour entrance. This effect is seen in miniature in Holes Bay where the south arm of Backwater Channel at the mouth of the bay deepened between 1954 and 1995, while the east and west arms shoaled (the deepening in the east arm between 1954 and 1980 was probably the result of land reclamation for road construction) (Figure 4).

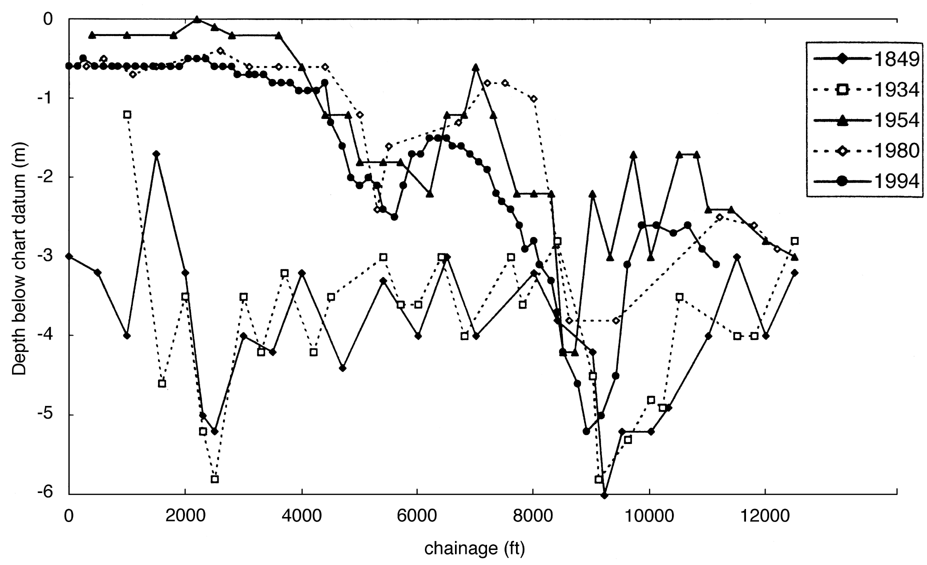

Figure 2 Changes in the profile of Wareham Channel. The chainage line runs from just north of Gigger's Island (0 feet) to the shore just north of Lake Pier (12,000 feet).

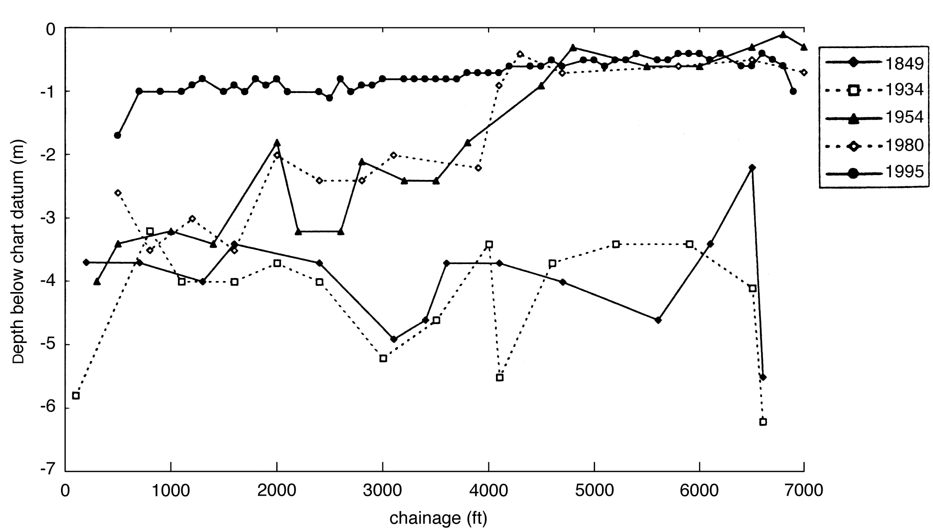

Figure 3 Changes in the profile of Wych Channel. The chainage line runs from east of Brownsea Island (0 feet) in a north-easterly direction and from 4000 feet runs east to Shipstal Point (7000 feet).

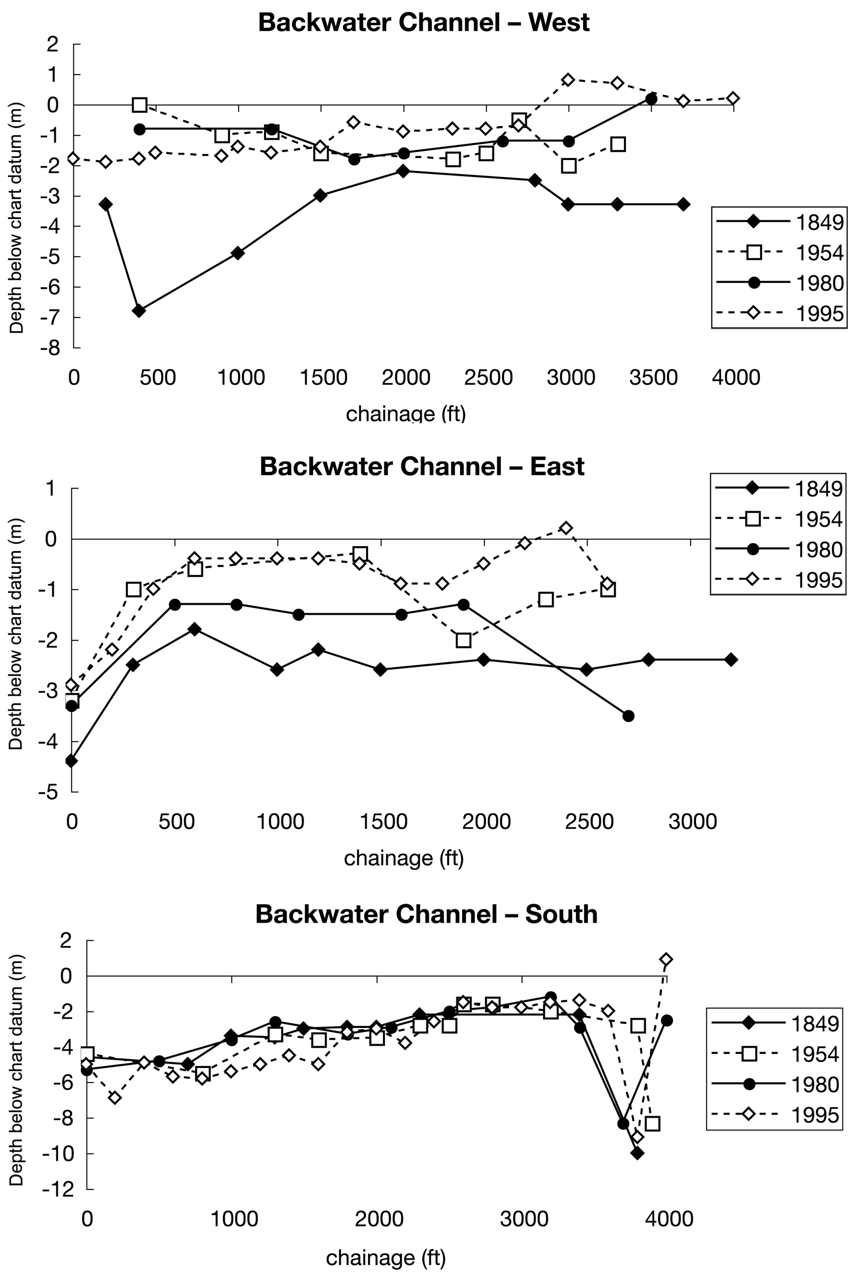

Figure 4 Changes in the profiles of channels in Holes Bay. The south chainage line runs from Poole Bridge (0 feet) to the centre of the bay. The east and west chainage lines are 'L' shaped running from the mouth of the south channel to the railway causeway.

An exception to the general deepening of the harbour is Upper Wych Channel (Figure 3). Between 1980 and 1995, the average depth of the channel changed from 1.7 m to 0.75 m. The effect was most marked in the lowermost 4000 feet (chainage 0 to 4000 feet) where the average depth was 2.6 m in 1980, but only 0.9 m in 1995.

In general, estuaries such as Poole Harbour reduce in volume over time as they act as 'settlement tanks'. The long-term trend in the channel depths before the introduction of *Spartina* was, therefore, probably a slow shoaling. As the sediment from eroding *Spartina* marshes is redistributed, the deepening may reverse and shoaling may begin again. In the future, the perturbation of channel depths caused by *Spartina* may be viewed as a blip in a long-term trend. Nevertheless, *Spartina* has had a remarkable influence on processes normally determined by large-scale physical factors.

Ecological change associated with *Spartina* in Poole Harbour

Vegetation changes

Throughout most of its range, *S. anglica* is found in a zone immediately seaward of other saltmarsh communities (Gray *et al*., 1991). *Spartina* was able to colonize this 'vacant niche' (Gray, 1986b) because of its greater ability to oxidize toxins (e.g. sulphides and ferrous compounds) and to tolerate salinity, flooding and sediment accretion (Gray *et al*., 1991). The pattern of spread in Poole Harbour (Hubbard, 1965) is consistent with colonization of bare mud, followed by invasion by other species from the landward edge of the sward.

Before the arrival of *S. anglica*, *Puccinellia maritima* was the commonest perennial plant in the lowest zones of saltmarshes in western Europe. In some areas, *Spartina* invaded *Puccinellia*, while in others *Puccinellia* invaded *Spartina*. In Great Britain, *Puccinellia* generally replaces *Spartina* in north-western saltmarshes (e.g. in Morecambe Bay). This effect is at least partly a result of the species' different mechanisms of photosynthesis, which cause *Puccinellia* to begin spring growth earlier at low temperatures and shade emerging *Spartina* shoots (Scholten and Rozema, 1990). The change from clayey and muddy substrate in the south and east to sandy substrates in the north-west is also a factor in the latitudinal change in the interaction between *Spartina* and *Puccinellia* (Scholten and Rozema, 1990). *Puccinellia* has invaded some *Spartina* marshes in Poole Harbour (e.g. Keysworth and east Lytchett Bay, Gray, 1986a), although the pattern of *Puccinellia* invasion is probably not associated with substrate variation (A. J. Gray, pers. comm.). The commonest other plant growing within *Spartina* is *Atriplex portulacoides*, which has invaded marshes in Parkstone Bay, Lytchett Bay, Brands Bay and Middlebere (Gray, 1986a; and see above).

At Keysworth, *Spartina* did more than just colonize bare mud. Studies of the stratigraphy of the area by Hubbard and Stebbings (1968) showed that the area was colonized successively by *Potamogeton pectinatus* (Fennel Pondweed), *Ruppia cirrhosa* (Spiral Tasselweed), *R.*

maritima (Beaked Tasselweed) and *Zostera* spp. (eelgrasses). The succession of these species suggests a gradual transition from freshwater to sea water, associated with a rise in sea level and/or a drop in land level. *Spartina* was found at -0.96 m OD beneath the oldest part of the Keysworth marsh, which is about 1 m below the present lower limit. This suggests that there was considerable compaction of the marsh substrate, causing the remains of the initial colonization to sink to a much lower level (Hubbard, 1965).

The effect of *Spartina* on wading birds

Poole Harbour is the most important estuary for wildfowl in Dorset, and supports nationally important populations of several species. The Black-tailed Godwit and Shelduck populations are of international importance (Prater, 1981). Ducks generally feed in Brands Bay, Newton Bay and at Arne, although the Bar-tailed Godwit prefers sandier areas such as Sandbanks (Gray, 1986a). Waders feed in these areas and also in the Wareham Channel and Holes and Lytchett Bays. As with other estuaries in southern England, double high tides in Poole Harbour tend to reduce the feeding time available to intertidal birds, compared with similarly sized areas in other parts of the country (Prater, 1981).

The spread of *Spartina anglica* on mudflats has been implicated in the decline of wader (particularly Dunlin *Calidris alpina*) populations in many British estuaries (Goss-Custard and Moser, 1988; Davis and Moss, 1984; Millard and Evans, 1984) because their invertebrate prey species decline and/or are less accessible within *Spartina* swards compared with bare mudflats. However, Goss-Custard and Moser (1988) found no evidence of an increase in Dunlin numbers in areas where *Spartina* was receding. Indeed in the Solent, Dunlin numbers declined during the 1970s and 1980s in spite of *Spartina* decrease (Tubbs *et al*., 1992).

One possible reason why waders have not increased in areas that have lost *Spartina* is a lag between *Spartina* recession and recolonization by wader prey species. Poole Harbour was one of the first estuaries to lose large areas of *Spartina* and so may be expected to be one of the first to show recovery of bird numbers if former *Spartina* marshes can revert to wader feeding grounds.

Peak wader counts for Poole Harbour for winters between 1969–70 and 1993–94 were obtained from the British Trust for Ornithology's annual reports of the Birds of Estuaries Enquiry (BoEE). The counts are shown in Figure 5. A rank correlation shows a highly significant upward trend in wader numbers ($r_S = 0.633$, $P < 0.01$). An exponential regression of number on year was also highly significant ($b = 0.0301$, $R^2 = 41.5\%$, $P < 0.001$) and showed an average annual percentage increase of 3.01% in wader numbers.

To test further the association between total wader numbers and *Spartina*, counts were obtained from BoEE reports for 14 other British estuaries which had continuous runs of data between 1971–72 and 1993–94. For each estuary the following calculations were made (Table 4):

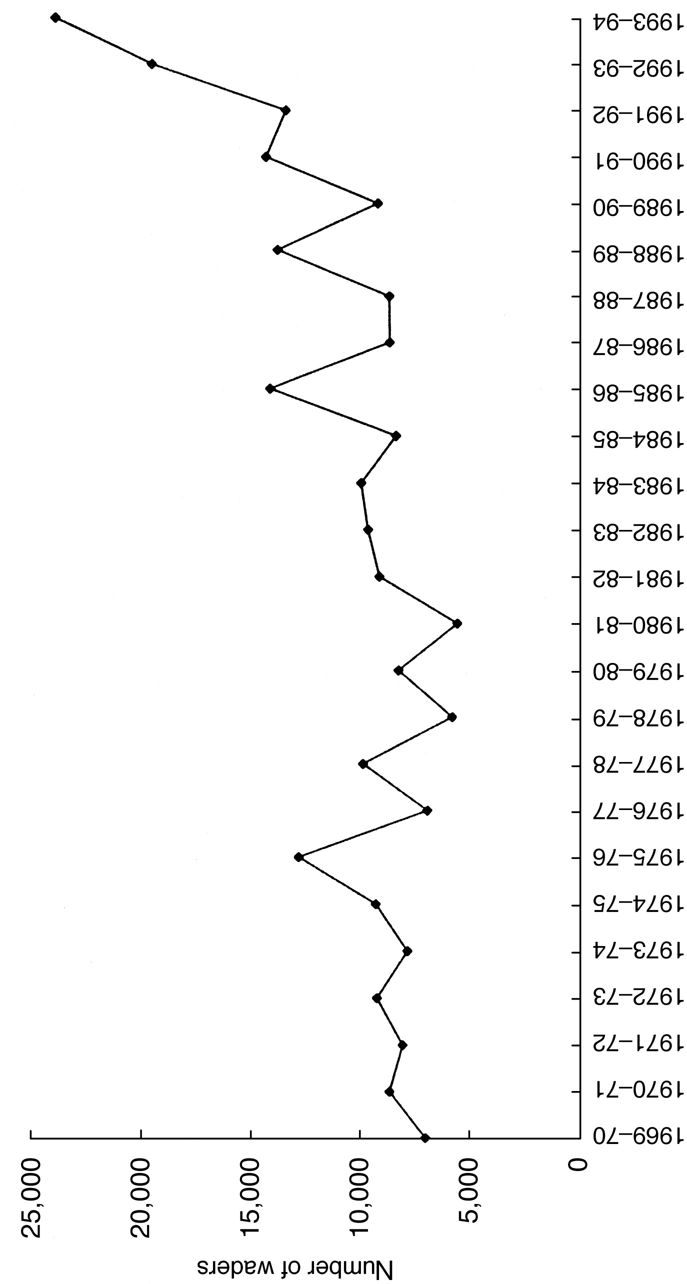

Figure 5 Changes in the total number of waders wintering in Poole Harbour.

Table 4 Changes in wader numbers and *Spartina* cover in Poole Harbour and other estuaries

Estuary	r_s	ARI %	Minimum count (thousands) (year)	Maximum count (thousands) (year)	*Spartina* area (1) (ha)	*Spartina* area (2) (ha)
Increased *Spartina* cover						
Exe	-0.388	-1.33	11 (1982–83)	26 (1969–70)	6	24
Chichester Harbour	-0.097	0.88	17 (1970–71)	45 (1989–90)	715	815
Severn	-0.522	-2.52	34 (1986–87)	131 (1973–74)	303	383
Morecambe Bay	-0.437	-1.36	105 (1982–83)	269 (1973–74)	185	368
Lindisfarne	-0.617	-3.19	19 (1984–85)	62 (1978–79)	36	127
Reduced *Spartina* cover						
Langstone Harbour	0.441	1.62	16 (1970–71)	46 (1989–90)	193	65
Medway	0.768	5.81	5 (1979–80)	54 (1992–93)	278	76
Blackwater	0.524	3.65	11 (1972–73)	78 (1992–93)	469	35
Stour (Essex)	0.718	3.09	14 (1971–72)	46 (1992–93)	149	119
The Wash	0.656	3.43	85 (1975–76)	353 (1992–93)	1914	138
Burry Inlet	-0.137	-0.76	18 (1978–79)	40 (1973–74)	405	335
Dee (Cheshire)	-0.267	-0.01	17 (1978–79)	158 (1992–93)	405	321
Humber	0.760	4.33	38 (1972–73)	127 (1989–90)	162	120
Ribble	0.060	-0.08	54 (1983–84)	219 (1973–74)	405	330
Poole Harbour	**0.633**	**3.01**	**6 (1980–81)**	**24 (1993–94)**	**600**	**350***

Spartina cover (1) from Hubbard and Stebbings (1967) and (2) from Burd (1989) except *from Gray *et al*. (1991).
r_s = rank correlation between winter peak wader numbers and time.
ARI = annual rate of increase of the winter peak wader count.

(i) rank correlation between bird number and year (tests for strength of trend)

(ii) exponential regression of bird number and year to find annual percentage rate of increase (tests for magnitude of trend)

(iii) the change in area of *Spartina* between the estimates of Hubbard and Stebbings (1967) and Burd (1989).

Estuaries were split into two groups, one for sites where *Spartina* had increased between the surveys of Hubbard and Stebbings and Burd (+*Sp*) and the other for sites where it decreased (-*Sp*). The differences in bird number trends between the categories were tested with a Mann-Whitney test, which ranks values and then tests whether the sum of the ranks in each category is significantly different from that expected if values had been assigned randomly to the categories.

There was a significant difference between the +*Sp* and -*Sp* categories in both the strength and magnitude of the positive trend in bird numbers. In the -*Sp* group were areas with the strongest positive trends (test of +*Sp* = -*Sp* vs +*Sp* < -*Sp* significant at $\alpha = 0.0042$) and the largest positive trends (+*Sp* = -*Sp* vs +*Sp* < -*Sp* significant at $\alpha = 0.042$). This relationship was not due to site latitude, because rank correlations of both coefficients and latitude were not significant (P = -0.182 and 0.122 for rank correlation and regression coefficients respectively; $N = 15$ in both cases). It is also worth noting that wader numbers declined in all estuaries with increased *Spartina* cover, whereas wader numbers increased nationally between 1987–88 and 1991–92 (Cayford and Waters, 1996). These results suggest an association between changes in *Spartina* cover and wader numbers, although changing *Spartina* cover is not necessarily the cause of the trends in wader numbers.

As suggested above, the lag between *Spartina* regression and recolonization of mud by wader prey species may be the reason previous studies found no increase in wader numbers in areas that had lost *Spartina.* McGrorty and Goss-Custard (1987) estimated the density of four wader prey species, *Hydrobia ulvae*, *Nereis diversicolor*, *Corophium* spp. and 'small bivalves' and calculated an invertebrate diversity index (IDI), a measure of the abundance and diversity of invertebrate prey species, for several sites in 1987.

The IDI for 10 sites is shown in Table 5. There is a statistically significant rank correlation between the IDI and the strength of the upward trend (significance of rank correlation coefficient) in wader numbers between 1971 and 1994 ($r_s = 0.728$, $N = 10$, $P = 0.05$–0.01) and the annual rate of increase in wader numbers over the same period ($r_s = 0.685$, $N = 10$, $P = 0.05$–0.01). McGrorty and Goss-Custard (1987) also found a significant relationship between the IDI and the annual rate of increase of Dunlin numbers between 1975 and 1986.

In conclusion, there was a significant increase in wader numbers in Poole Harbour over the 25 year period and there is circumstantial evidence that this was due to invertebrates recolonizing mudflats previously occupied by *Spartina*. The time between *Spartina* loss and recolonization by invertebrates may be over 20 years (McGrorty and Goss-Custard, 1987), which could explain why wader numbers do not increase immediately.

Table 5 Relationship between invertebrate prey species and change in wader numbers for 10 British estuaries

Estuary	r_s	ARI	IDI
Medway	0.768	5.81	79
Stour	0.718	3.09	75
Poole Harbour	**0.633**	**3.01**	**70**
Blackwater	0.524	3.65	70
Langstone Harbour	0.441	1.62	42
Chichester Harbour	0.097	0.88	75
Hamford Water*	0.067	0.70	63
Exe	-0.388	-1.33	63
South-west Solent*	-0.481	-1.31	58
Portsmouth Harbour*	-0.759	-4.89	46

*Data not continuous.

r_s = rank correlation between winter peak wader numbers and time.

ARI = annual rate of increase of the winter peak wader count.

IDI = invertebrate diversity index (see text).

Table 6 The frequency of ergot infection of *Spartina* inflorescences and spikelets in Poole Harbour

Year	Inflorescences infected (%)	Spikelets infected (%)
1983	36	–
1984	61	–
1985	80	16.1
1987	–	22.8
1988	85	–
1992	84	–
1995	71	23.6
1997*	90	23.0

Source: 1980s inflorescence data from Gray *et al.* (1990).

*Data from Brands Bay and Bramble Bush Bay only.

Spartina and the ergot fungus

Since the early 1980s, *Spartina* in Poole Harbour has become increasingly infected by the Ergot fungus *Claviceps purpurea* (Table 6). The life cycle has been described by Gray *et al.* (1990). The most obvious symptom of infection is the sclerotium or ergot, a mass of fungal hyphae which protrudes from an infected spikelet. The ergots overwinter in the surrounding mud and germinate in the spring, producing sexual ascospores which land on *Spartina* stigmas and lead to a primary infection. Secondary infection happens through dispersal of asexual conidiospores extruded from infected spikelets in a sticky honeydew. Development of sclerotia completes the life cycle.

The epidemic on *Spartina* in Poole Harbour is unusual, not so much for its high infection rate, but because of its persistence and uniformity. Other grass species such as *Lolium perenne* (Ryegrass) (Jenkinson, 1958) and *Spartina alterniflora* (Eleuterius and Meyers, 1974; Gessner, 1978) have high ergot infection rates, but these tend to be short-lived, confined to particular habitats within sites, or both. As Table 6 shows, the proportion of infected inflorescences in Poole Harbour remained at over 70% for 10 years. Also among 15 sites throughout the harbour (see Gray *et al*., 1990), there is no tendency for differentiation into populations with consistently high or low infection rates (Friedman two-way analysis of ranks S = 16.28, d.f. = 11, $P = 0.133$) (Raybould *et al*., 1998). There are no published long-term data sets for ergot infection of other *Spartina anglica* populations. However, Gray *et al*. (1990) reported observations of Thompson on the Dee estuary marshes, which suggest that a persistent infection was developing in the late 1980s. It seemed, however, that infection rates were consistently higher in the mature zone compared with the pioneer zone.

The probable reasons for the high, persistent and uniform infection rates in Poole Harbour are the genetic uniformity of *Spartina* (Raybould *et al*., 1991a), the lack of zonation of *Spartina* in the harbour, the closed nature of the harbour allowing the build up of inoculum, and perhaps the old age of many clonal lines (c.f. the mature zone on the Dee). The reduction in infection rate in 1995 compared with 1992 may be due to the hot summer of 1995 as ergot spread is favoured by cool, damp conditions (MAFF, 1974).

It is difficult to estimate whether the ergot is having a significant deleterious effect on *Spartina*. The most obvious potential effect is reduction in seed production. Raybould *et al*. (1998) found that in 1985 and 1995, there was no significant difference between the average number of seeds produced on uninfected and infected inflorescences. Although inflorescences with high ergot infection (more than 10% of inflorescences infected) produced fewer seed than uninfected inflorescences, the lower seed output was offset by inflorescences with light infection (fewer than 10% of spikelets infected) producing more seed compared with uninfected inflorescences. As Raybould *et al*. (1998) point out, these results do not necessarily mean ergot has no effect in reducing the actual (‘realized’) total seed output of *Spartina* in Poole Harbour from what it would have been in the absence of ergot infection (‘potential’ seed output) because ergot may not infect inflorescences at random. If ergot preferentially infects inflorescences that have the highest potential seed output, there may be no detectable difference in seed production between infected and uninfected inflorescences, but realized seed production from these inflorescences would be lower than the potential output.

Bacon and Luttrell (1981) used radioactive carbon dioxide to demonstrate that ergots developing on rye plants diverted resources from developing seed. Raybould *et al.* (1998) found that heavy ergot infection of *Spartina* was associated with lower mean seed weight. Therefore, high amounts of ergot may reduce seed quality as well as seed number. Nevertheless seed set is sporadic in *Spartina* and seedling recruitment is rare in mature marshes such as those in Poole Harbour. Therefore, reduction in seed set may have little effect on *Spartina* fitness, except in the long term when release of genetic variation through sexual reproduction may be beneficial (Gray *et al*., 1991).

A more immediately important effect of ergot may be diversion of resources from vegetative reproduction of the host. The mean weight of an ergot on a particular inflorescence was significantly negatively correlated with the number of ergots on the inflorescence in all years analysed (1986, 1988, 1992 and 1995) and variation in ergot number explained nearly three-quarters of the variation in mean ergot weight in 1995. This suggests resources are limiting ergot growth and so ergots may compete with the host for resources (Raybould *et al*., 1998). However, the total weight of ergot per inflorescence is very small (>100 mg), and it seems unlikely that the growth of *Spartina* is greatly affected by diversion of resources to ergots. It is possible, however, that ergots may influence vegetative reproduction in other ways, perhaps by the production of chemicals that affect growth.

Conclusions

There are many opinions about whether the spread of *Spartina* is beneficial or detrimental to saltmarshes and surrounding areas (Doody, 1990). One certainty is that *Spartina* is fascinating to evolutionary biologists and ecologists because it presents the opportunity to study the ecological effects of speciation. The spread of *Spartina* was a massive perturbation to the ecosystem of Poole Harbour. The events described in this chapter represent physical and biological adjustments to this perturbation. The interesting question now is whether the invasion/erosion sequence is cyclical, with *Spartina* reinvading its old habitats, or whether it will reach equilibrium, perhaps at a much lower area of *Spartina*. The appearance of ergot infection is especially interesting as it indicates evolutionary as well as ecological change may now be occurring in response to the arrival of *Spartina*.

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